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Are 50-kHz calls used as play signals in the playful interactions of rats? II. Evidence from the effects of devocalization

Theresa M. Kisko*, Brett T. Himmler, Stephanie M. Himmler, David R. Euston, Sergio M. Pellis

Department of Neuroscience, University of Lethbridge, Lethbridge, Alberta, Canada

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ABSTRACT

During playful interactions, juvenile rats emit many 50-kHz ultrasonic vocalizations, which are associated with a positive affective state. In addition, these calls may also serve a communicative role – as play signals that promote playful contact. Consistent with this hypothesis, a previous study found that vocalizations are more frequent prior to playful contact than after contact is terminated. The present study uses devocalized rats to test three predictions arising from the play signals hypothesis. First, if vocalizations are used to facilitate contact, then in pairs of rats in which one is devocalized, the higher frequency of pre-contact calling should only be present when the intact rat is initiating the approach. Second, when both partners in a playing pair are devocalized, the frequency of play should be reduced and the typical pattern of playful wrestling disrupted. Finally, when given a choice to play with a vocal and a non-vocal partner, rats should prefer to play with the one able to vocalize. The second prediction was supported in that the frequency of playful interactions as well as some typical patterns of play was disrupted. Even though the data for the other two predictions did not produce the expected findings, they support the conclusion that, in rats, 50-kHz calls are likely to function to maintain a playful mood and for them to signal to one another during play fighting.

1. Introduction

When rats are engaged in social play they emit ultrasonic vocalizations (USVs) (Burgdorf et al., 2008; Knutson et al., 1998). These vocalizations are typically in the 50-kHz range and usually of the frequency modulated (FM) subtypes of 50-kHz USVs (Burgdorf et al., 2011; Wöhr et al., 2008; Wright et al., 2010). In non-playful contexts, calls have been shown to attract approach by other rats (Wöhr and Schwarting, 2009, 2012) and recently, it has been found that these vocalizations are more frequent before playful contact is made than when such contact is terminated (Himmler et al., 2014). These findings suggest that, during playful interactions, FM 50-kHz USVs may be being used as play signals to promote and maintain play. If USVs are acting as play signals, then playful interactions between rats should be disrupted in their absence. Indeed, it has been found that in deafened rats the close quarter wrestling component of play is significantly diminished, although the frequency of play initiation remains unchanged (Siviy and Panksepp, 1987).

Play signals have been reported in many species. Some of the best known include the play bow of dogs (Bekoff, 1995) and the open-mouth play face of primates (Van Hooff, 1967). Play signals are frequently emitted prior to grabbing or biting the partner (Bekoff, 1995; Pellis and Pellis, 1997) and in situations in which there may be ambiguity in the actions performed during play, such as when multiple partners are involved or when there is a size or dominance asymmetry between the players (Bekoff, 1995; Fagen, 1981; Palagi, 2008; Palagi and Mancini, 2011; Van Leeuwen et al., 2011; Waller and Dunbar, 2005). Most play signals characterized to date involve the visual modality, such as the play bow and the open-mouth play face mentioned above. However, several examples of possible play signals involving vocalizations have been reported (Biben and Symmes, 1986; Masataka and Kohda, 1988; Rasa, 1984). Kipper and Todt (2002) showed that playful vocalizations in Barbary macaques are more frequent preceding an attack than following contact and also that different variants of these calls are emitted at different times during the encounter. As noted above, we previously found a similar pattern with regard to 50-kHz calls in rats when they are playing (Himmler et al., 2014).

* Corresponding author at: AG-Schwarting, Fachbereich Psychologie (04), Gutenbergst. 18, 35032 Marburg, Germany.
E-mail address: Theresa.Kisko@gmail.com (T.M. Kisko).

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In nocturnal animals, such as rats, visual signals are likely not as useful as vocal ones. For example, nocturnal primates have a richer vocal repertoire and a more limited visual repertoire than do diurnal ones (Braune et al., 2005; Zimmermann, 1995). USVs emitted by rodents dissipate easily, allowing communication with a reduced risk of being detected by predators (Brudzynski, 2009), thus making 50-kHz calls low risk signals to communicate play. In addition, in rats, not only are 50-kHz calls divided into flat and FM modulated ones, but also the latter are made up of at least 14 different variants (Wright et al., 2010), providing the potential for different calls or combination of calls serving different communicatory functions.

During playful interactions, rats attack and defend the nape of neck, which if contacted is nuzzled (Pellis and Pellis, 1987; Siviy and Panksepp, 1987). The tactics used to defend against nape contact can either promote bodily contact in the form of wrestling or decrease the chance of contact by withdrawing from the attacker (Pellis and Pellis, 1987). Bodily contact has been shown to increase the occurrence of 50-kHz USVs (Burgdorf and Panksepp, 2001; Cloutier et al., 2012; Knutson et al., 2002; Panksepp and Burgdorf, 2000), increasing the likelihood that these calls could be used as play signals to encourage further bodily contact with the other animal. The present study uses rats that have been devocalized, and so unable to produce USVs, so as to test three predictions to evaluate whether these calls are used as play signals.

If the 50-kHz calls function as traditionally envisaged play signals – signifying "I want to play with you" (Bekoff, 1975, 1995), then they should be emitted more frequently immediately before contact is made than immediately after terminating contact. As already noted, this is the case (Himmler et al., 2014). However, play signals may be multi-functional, signaling not only approach, but also withdrawal from the partner and, in some cases, being used for self-communication by the performer (Pellis and Pellis, 1997, 2011; Pellis et al., 2011). In fact, in our previous study, we found that even though one particular type of FM call, the trill, was most often emitted during play, a finding consistent with other studies (Snoeren and Amgo, 2013; Wright et al., 2010), different FM calls were associated with withdrawal compared to approach (Himmler et al., 2014), suggesting a difference when signaling contact to come versus termination of contact (Pellis and Pellis, 1997). Therefore, while consistent with the traditional view of play signals (i.e., signals that promote playful contact), the significantly higher frequency of calls prior to contact may also be consistent with alternate hypotheses.

The main problem with measuring vocalizations in fast-paced, dynamic playful interactions is that any one call cannot readily be attributed to a specific member of the playing pair. Thus, while it is a reasonable inference, given the traditional play signals hypothesis, that the increased frequency of calls present prior to contact arises from the attacking partner, it cannot be concluded to be so with certainty, as both rats could be potentially calling. Therefore, the first prediction tested in this paper is that, if the calling is used to announce imminent contact by the attacker, then the higher frequency of calling prior to contact should arise because the attacker calls more. To test this, calling during play in pairs in which one partner of a playing pair was devocalized was evaluated. The specific prediction was that when the attacker is the non-vocal animal, then there should be no difference in the frequency of calling before contact and immediately after contact is terminated – both should be low. In contrast, when the attacker is able to vocalize, then there should be a significantly higher frequency of calling immediately before contact than immediately after, as previously found (Himmler et al., 2014).

If vocalizations are promoting playful interactions, then in their absence the frequency of playful contact should decrease. Knutson et al. (1998) showed that over the course of a test trial, the frequency of emitting 50 kHz calls is correlated with the waxing and waning of nape contact, but not with wrestling. In seeming opposition to these findings, Siviy and Panksepp (1987) showed that when pairs of rats are deafened, they will initiate playful contact just as often as intact rats, but are significantly less likely to wrestle with one another. Eliminating hearing, however, is not the same as eliminating vocalizations. Rats that are deaf not only cannot hear vocalizations, but also cannot hear other auditory cues from their partner that are potentially important, such as footsteps and breathing (Beatty and Costello, 1983; Pellis et al., 1996; Pellis et al., 1992; Thor & Holloway, 1982). Thus, a deaf rat may misjudge the proximity of their partner and reduce the likelihood of engaging in a defensive tactic that promotes wrestling. A more direct way to determine if it is, in fact, the USVs that are responsible for either facilitating playful contact or wrestling is to eliminate the rat's ability to emit USVs. Therefore, for the second prediction in this paper, we expected that, if USVs are critical for facilitating play, then when both play partners are devocalized, there should be a reduction of nape attacks, wrestling or both. To test this, the play of pairs of devocalized rats was compared to the play of sham-treated control rats.

When given the option, rats prefer to socialize with a partner that emits many 50-kHz calls than one that emits few (Wöhr et al., 2008; Wöhr and Schwarting, 2009), and in playback experiments, rats will spend more time around the speaker emitting 50-kHz vocalizations (Burgdorf et al., 2008; Sadananda et al., 2008). However, the role of vocalizations in attracting play partners has not previously been studied. Given that rats find 50-kHz calls attractive, for the third prediction of this paper, it was expected that, when given a choice, rats would preferentially initiate play with a partner that can vocalize. To test this prediction, quads of rats, with two devocalized and two intact, were placed together in the testing enclosure. If vocal partners are more attractive, then it should be the case that all the rats will prefer to initiate play with a partner that can vocalize and will avoid initiating play with ones that do not.

2. Methods and materials

2.1. Subjects

Sixty-four male Long Evans rats were used. The rats were obtained from Charles River Laboratories (St. Constant, Quebec) around 23 days of age and housed in the vivarium at the Canadian Centre for Behavioral Neuroscience. They were housed in quads with food and water available ad libitum and were on a 12-hour light–dark schedule, lights off at 1930. The animals were maintained at a constant temperature of around 21–23 °C and were housed in polyethylene cages 46 cm × 25 cm × 20 cm with processed corncob as bedding. Devocalization and the sham surgeries were performed when the rats were at or between 28 and 30 days of age, with half of the quads having two members devocalized and half sham-treated. The rats remained in their respective quads after surgeries and testing for play occurred when they were between 35 and 40 days old, the age when juveniles are most playful (Pellis and Pellis, 1990; Thor and Holloway, 1984).

2.2. Apparatus

Testing took place in a 50 cm × 50 cm × 50 cm clear Plexiglas enclosure which was placed into a sound proof box (inside measurements: 59 cm × 65.5 cm × 81.5 cm). The inside of the play box was filled with approximately 1–2 cm of CareFresh® bedding, as this bedding emits less background noise when walked on by the rats during recording compared to standard corncob bedding. The sound proof box was fitted with sound-attenuating foam